

NESTING BIOLOGY OF THREE ALLODAPINE BEES IN THE SUBGENUS *EXONEURELLA* MICHENER (HYMENOPTERA: ANTHOPHORIDAE)

by T. F. HOUSTON*

Summary

HOUSTON, T. F. (1977) Nesting biology of three allodapine bees in the subgenus *Exoneurella* Michener (Hymenoptera: Anthophoridae). *Trans. R. Soc. S. Aust.* 101(4), 99-113, 31 May, 1977.

Results of a detailed study of nest populations of *Exoneura* (*Exoneurella*) *tridentata* are presented with less complete observations of *E. (E.) eremophila* and *E. (E.) setosa*. These species rear their larvae progressively in open burrows in dead plant stems, *tridentata* in ready-hollowed woody twigs, *eremophila* and *setosa* in pithy herbaceous stems. *E. tridentata* exhibits small semisocial colonies with queen and worker castes. The castes are dramatically morphologically dissimilar, the large-bodied queens appearing flightless and restricted to nests. By contrast, colonies of *eremophila* and *setosa* are basically subsocial. The subsocial condition in these species may be derived from a semisocial condition and possibly associated with life in rapidly perishable stems.

An unidentified encyrtid wasp, reared from pupae of *tridentata*, was found in association with the bees.

Introduction

The bulk of this paper presents the results of a study of the nesting biology of *Exoneura tridentata*. The remainder presents less complete data on the biologies of *E. eremophila* and *E. setosa*. These three species were described only recently (Houston 1976) and nothing hitherto has been recorded of their bionomics. With *E. lawsoni* Rayment, they comprise the subgenus *Exoneurella* (sometimes accorded generic status) and belong to the group of bees termed allodapines (after *Allodupe*). A general account of the biology of allodapine bees is given by Michener (1974). Most species make their homes in burrows in pithy stems or twigs or in dead wood. They construct no cells but raise their immatures together in the common nest chamber. Usually the larvae are fed progressively to maturity by the adult females. Most allodapines display primitive social behaviour in at least part of their life cycle, two or more females occupying one nest and exhibiting division of labour. One female functions as an egg layer (or queen) and seldom forages, while one or more other females with undeveloped ovaries function as workers, foraging and tending the brood.

Michener (1964) considered *E. lawsoni* to be essentially 'solitary' (really subsocial) although several other species of *Exoneura* are semisocial (Michener 1965). He postulated that the 'solitary' habits of *E. lawsoni* were probably derived from a semisocial condition and not primitive. The new information on close relatives of *E. lawsoni* presented below is considered in relation to this problem.

The study of *E. tridentata* was prompted by discovery of the first nests which contained relatively huge females amongst normal-sized individuals (cf. Figs 1A, 1B). Female size variation and allometry in this species is described by Houston (1976). Such variation is absent from other *Exoneurella*.

Exoneura tridentata Houston

Methods

All nest material was collected from north-eastern Eyre Peninsula, S. Aust., and the greater part of it from the Lake Gilles National Park, 110 km SW of Port Augusta. Nest collection was carried out during early morning, late evening or during cool rainy periods when all occupants should have been present.

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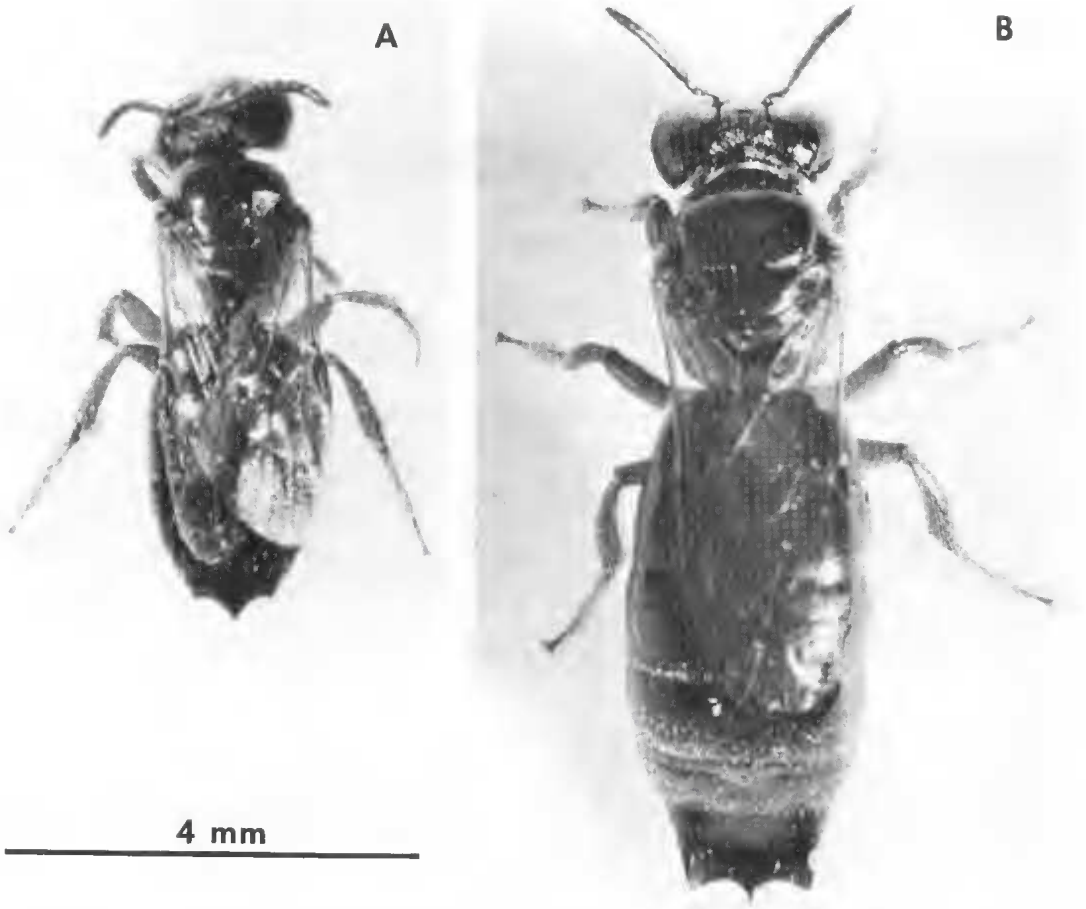


Fig. 1. Females of *Exoneura tridentata* (both to same scale). A. Small minor (pinned). B. Large major (live).

Nest contents were observed alive and then preserved as soon as practicable after collection in 70% ethyl alcohol.

Adult females were measured, examined for wing wear and most were dissected to determine ovary condition and whether or not mating had occurred. Wing wear was rated 0 (margins entire), 1 (one to three nicks), 2 (four to ten nicks), 3 (over ten nicks), 4 (badly tattered). Ovary size was rated 1 (ovaries tiny, slender and borne on long oviducal stalks), 2 (slightly enlarged), 3 (moderately enlarged), 4 (large, at least one ovum near egg size). The length of the largest ovum of each female was also measured.

General observations

Nests

Adults of *E. tridentata* utilise ready made burrows in dead woody twigs or branches of standing trees for both shelter and brood rearing. The term 'nest' is used below to denote burrows used for brood rearing. Shelters are virtually identical except that they are not always cleared of debris, especially when occupied solely by males.

Except for one nest in a branch of native pine (*Callitris* sp.), all occupied tunnels were in dead twigs and branches of Bullock Bush (*Heterodendrum oleaefolium* Desf.), a common small tree of semi-arid southern Australia.

The lower branches of the trees are commonly dead and prone to attack by beetle larvae which bore through the centres of the twigs. Searches of other shrubs and trees revealed very few hollows which the bees might utilise.

Occupied tunnels were 0.6–2.0 m above ground, 2–4 mm in diameter and 25–628 mm in length (most were shorter than 100 mm). They were inclined at various angles from horizontal to about 45° from vertical. Their entrances were either terminal in the ends of broken twigs or lateral but none opened directly upwards so that rain might enter. Entrances were unmodified, showing no traces of the collars of compacted plant material that characterise nests of most other allodapines.

Some tunnels with lateral entrances were double-ended and the bees occupied just one or both ends. In one case (nests 26, 27, Table 1) it appeared that two independent nests had been established in opposite ends of a common burrow.

All nests collected in December and October contained an amorphous patch of dry pollen covering the wall of one side between the brood and the entrance. The patches varied from the merest smear to thick masses up to 30 mm long. Some were composed of one kind of pollen, others of two or more kinds. The quantity of pollen in some nests leaves little doubt that the bees had been accumulating it as a food store and had not simply deposited it accidentally while preparing provisions for the larvae.

Nests collected at other times lacked fresh pollen stores, although a few contained old mould-encrusted ones. The absence of pollen stores from these nests cannot be attributed to lack of flowers for they occurred in abundance at the time of collection. More probably the limited fine weather suitable for foraging was insufficient to allow accumulation of surplus pollen.

Immatures

A description of the immature stages is given by Houston (1976). All occurred loosely within the tunnels. Eggs usually lay crisscrossed or jumbled in the closed ends regardless of the inclination of the tunnels. First and second instar larvae which remain partially enclosed in their chorions were found near the closed ends of the tunnels often amongst eggs. Later instars and pupae were arranged in order of increasing age towards and facing the nest entrances.

A few 3rd and 4th instars were found feeding on moist pollen masses adhering to their venters. However, most larvae were without food, probably because weather conditions at and preceding nest collection were not conducive to flight and food gathering.

The durations of immature stages were not determined. The numbers of each stage found in nests are listed in Table 1.

Eggs exhibited considerable size variation even within nests. A pronounced seasonal shift in average egg size was also noted (Fig. 2) so that the size/frequency distributions of the June and October samples barely overlap. The cause of this shift is unknown.

Parasites

The only organism found associated with nest colonies of *E. tridentata* was an unidentified species of minute encyrtid wasp. Larvae of the wasp developed within the bodies of young bee pupae, completely consuming all tissue except the cuticle. Parasitised pupae eventually became filled with numerous wasp larvae which pupated within the host cuticle. Adult parasites emerged through holes chewed through the cuticle.

Of 74 bee pupae collected in December, 39 (53%) were killed by encyrtids, both sexes being equally affected. As no pupae were found in other nest samples the period of activity of the parasite was not determined.

Food sources

E. tridentata is polylectic and has been found collecting pollen from *Amyema*, *Eremophila*, *Eucalyptus* and *Melaleuca*.

Colony composition

A colony may be defined as the living inhabitants of a single nest. The composition of each colony found is shown in Table 1. The smallest of these colonies comprised a lone female with one egg (nest 36). Most nests, however, contained two or more adult females, a maximum of 20 occurring in nest 42. This nest also contained an adult male and 46 immatures (mostly eggs) making it one of the most populous found.

As mentioned above, some tunnels with lateral entrances were double-ended. In one such case, 2 separate colonies (nests 26, 27) were recognised, separate groups of adults and immatures occupying opposite ends of the tunnel. In a second case (nest 22), adults occupied both ends while immatures occurred only at one end. This group was treated arbitrarily as a single colony.

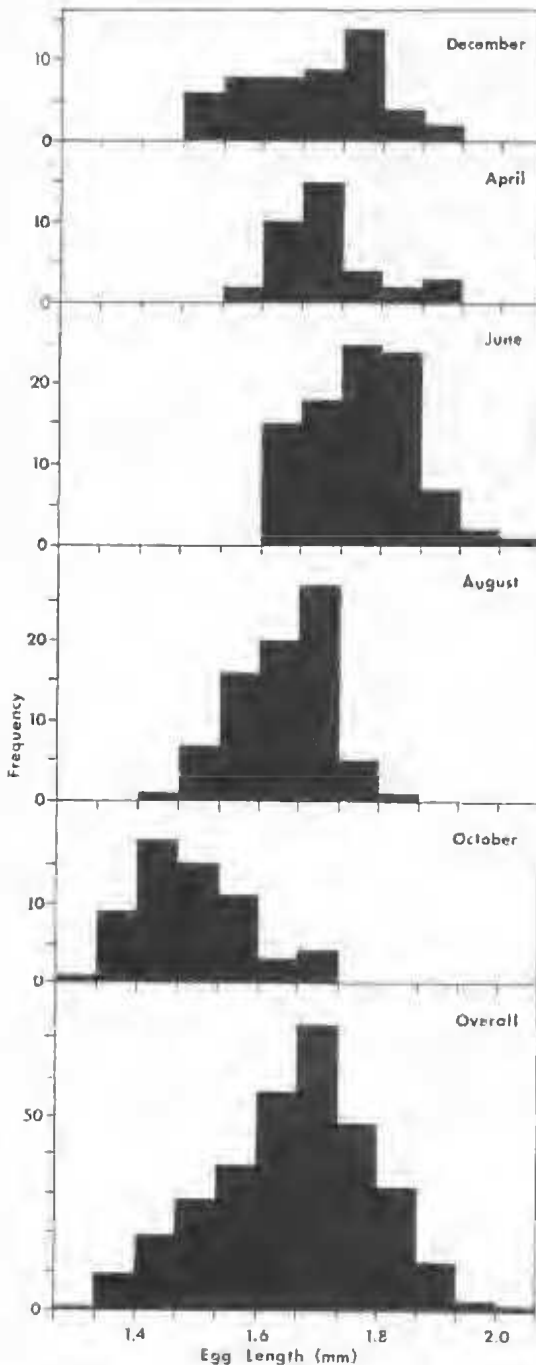


Fig. 2. *Exoneura tridentata*. Histograms showing egg size frequency distributions for different nest samples.

Nest data reveal that brood rearing and production of both sexes occur year round. Eggs, larvae and adults of both sexes were

present in all samples. As pupae occurred only in the December sample, one might suspect that eggs and larvae collected in the relatively cool inclement months of April-September were dormant. However, some adults in the June sample were teneral and had obviously just emerged from pupae. Additionally, some adult females in all samples had ova of or near egg size.

Every nest contained one or more eggs so that egg production must occur intermittently throughout the life of a colony. Were it otherwise, eggs would not be expected in nests with advanced progeny. With such continuous egg production, larval hatching should also occur continuously so that there ought to be no intermediate age gaps in series of immatures. However, it will be seen from Table 1 that many series do have intermediate gaps (e.g. nests 2-4, 8, 26). The rarity of 1st instars is particularly obvious but might be explained by their brief duration (1st instars are non-feeding). The absence of later instars must be attributed to mortality. Perhaps adults occasionally eat eggs or young larvae: eating of eggs has been reported amongst allodapines by Michener (1974, p. 186).

Adult females greatly outnumbered adult males in nests. Males from nests showed little or no wing wear and presumably leave their natal nests while young. Many males were found singly or two or three together in twigs which did not appear to have served as nests. Of the pupae found, 56 were females and 18 were males suggesting a sex ratio of about 3:1.

Colony development appeared to be more or less synchronous. All 10 nests in the December sample contained pupae while none did in other samples. Nests of the April and August samples contained eggs but most lacked larvae. Such synchronisation is unexpected in a species breeding year round and obviously some environmental factor(s) regulates the breeding cycle. Winter cold cannot be the factor in view of the winter breeding. More probably it is the lack of suitable flowers at one or more times of the year which halts breeding and results in synchronisation.

Within single colonies adult females showed marked variation in size, age (as judged by wing wear) and ovarian condition; some were fertilized, others not. The data obtained from examination of females are too numerous to be tabulated individually and are summarised and analysed in the following two sections.*

* Copies of the data are obtainable from the author or the Librarian.

TABLE I

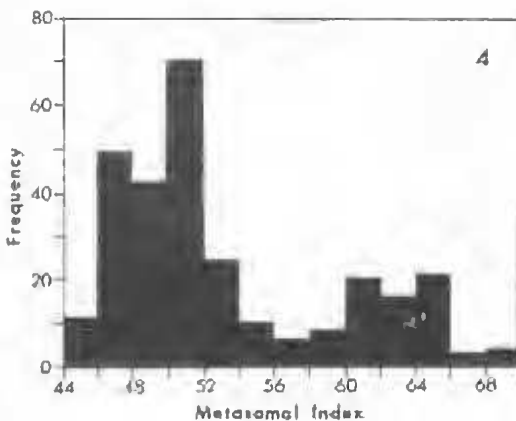
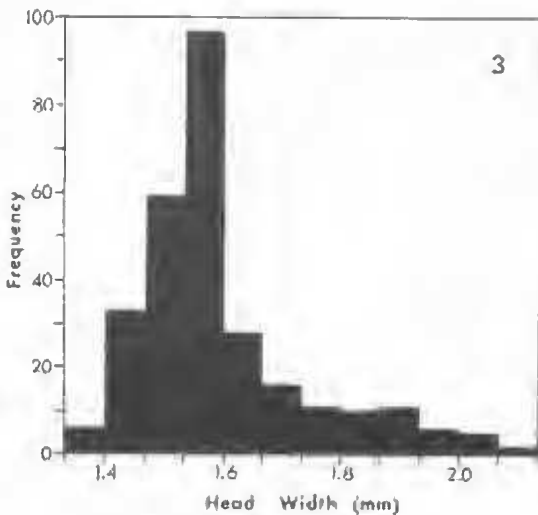
Exoneura tridentata. Contents of nest twigs collected at different times. Larvae were sorted into stadia (stadium v = prepupa). Numbers in the column on the extreme right assign each colony to one of the categories in Table 2. † indicates pupal series affected by encyrtids.

Date of collection	Nest no.	Eggs	Larvae					Pupae		Adults		Pollen store	Colony category
			i	ii	iii	iv	v	♀	♂	♀	♂		
19.iv.1971	1	4	—	—	—	—	—	—	—	14	1	—	II
30-31.xii.1973	2	1	—	—	1	2	3	1	—	6	—	+	IV
	3	5	—	—	1	1	—	6†	—	4	3	+	III
	4	6	—	—	1	—	2	3	—	2	1	+	III
	5	2	—	I	1	1	—	3	1	5	1	+	II
	6	2	—	1	2	—	2	2†	2†	3	—	+	II
	7	11	—	1	1	4	2	18†	5†	9	—	+	IV
	8	1	—	—	—	—	1	3	3	3	2	+	V
	9	12	—	2	2	6	2	13	2	13	1	+	IV
	10	4	—	1	1	—	—	6†	4†	5	2	+	III
	11	4	—	2	1	1	2	—	1	3	2	+	II
11-16.iv.1974	12	4	—	—	—	—	—	—	—	5	—	—	V
	13	4	—	—	—	—	—	—	—	7	—	—	II
	14	4	—	1	—	2	—	—	—	15	1	—	III
	15	3	—	—	—	—	—	—	—	6	1	—	IV
	16	2	—	—	—	—	—	—	—	2	—	—	V
	17	2	—	—	—	—	—	—	—	4	—	—	III
	18	10	—	—	—	—	—	—	—	5	2	—	II
	19	1	—	—	—	—	—	—	—	5	—	—	V
	20	10	—	1	—	1	—	—	—	10	—	—	IV
	21	8	—	—	—	—	—	—	—	4	—	—	III
22	7	—	—	—	—	—	—	—	13	—	—	IV	
14-17.vi.1974	23	23	—	6	—	—	—	—	—	15	2	—	III
	24	13	3	1	—	—	—	—	—	10	—	—	V
	25	9	—	—	—	—	—	—	—	6	—	—	V
	26	5	—	—	—	4	—	—	—	8	3	—	V
	27	27	1	6	6	12	—	—	—	9	7	—	III
	28	16	—	3	—	1	—	—	—	6	2	—	III
	29	2	—	—	—	—	—	—	—	2	—	—	VI
29.viii-I.ix.1974	30	2	—	—	—	—	—	—	—	1	—	—	VI
	31	20	—	2	—	—	—	—	—	14	—	—	III
	32	2	—	1	—	—	—	—	—	2	—	—	III
	33	14	—	1	—	—	—	—	—	7	2	—	III
	34	5	—	—	—	—	—	—	—	3	—	—	II
	35	4	—	—	—	—	—	—	—	1	—	—	I
	36	1	—	—	—	—	—	—	—	1	—	—	I
	37	11	—	1	—	—	—	—	—	4	1	—	III
	38	8	—	1	1	1	—	—	—	3	—	—	V
	39	5	—	—	—	—	—	—	—	2	—	—	V
	40	5	—	—	—	—	—	—	—	2	—	—	III
27.x.1974	41	8	—	2	1	1	—	—	—	5	2	+	IV
	42	32	—	5	3	6	—	—	—	20	1	+	III
	43	2	—	2	1	—	—	—	—	1	—	+	I
	44	23	—	4	3	2	—	—	—	10	—	+	V

Evidence of female castes

In many colonies one adult female was conspicuously larger than the remainder. In some other nests the females were more graded in size but smaller females outnumbered the larger ones. The size/frequency distribution of twig inhabiting females is strongly skewed (Fig. 3) reflecting the relative abundance of the smaller size classes.

As explained by Houston (1976) females exhibit allometry where the metasoma is proportionately greater in large females than in small ones (cf. Figs 1A, 1B). This difference may be quantified by the 'metasomal index': the ratio of the distance between the lateral projections of the 6th metasomal tergum to the head width. The frequency distribution of metasomal indices (Fig. 4) is distinctly bimodal. Thus two



Figs 3, 4. *Exoneura tridentata*, Fig. 3.—Histogram showing strongly skewed frequency distribution of adult female head widths. Fig. 4.—Histogram showing bimodal frequency distribution of metasomal indices of adult females.

partially distinct morphs may be recognized, termed here 'minors' (metasomal index 57 or less) and 'majors' (metasomal index 58 or more).

Majors made up 25% of the total sample of females. In individual samples the percentages were: December, 27%; April, 23%; June, 31%; August, 23% and October, 22%.

The ovaries of most females taken from twigs were examined. Those rated 1 (tiny with stalk-like oviducts) were considered inactive while those rated 2-4 (small to large) were considered active. The relationship between ovarian activity and metasomal index (Fig. 5) suggests that ovarian activity is more frequent

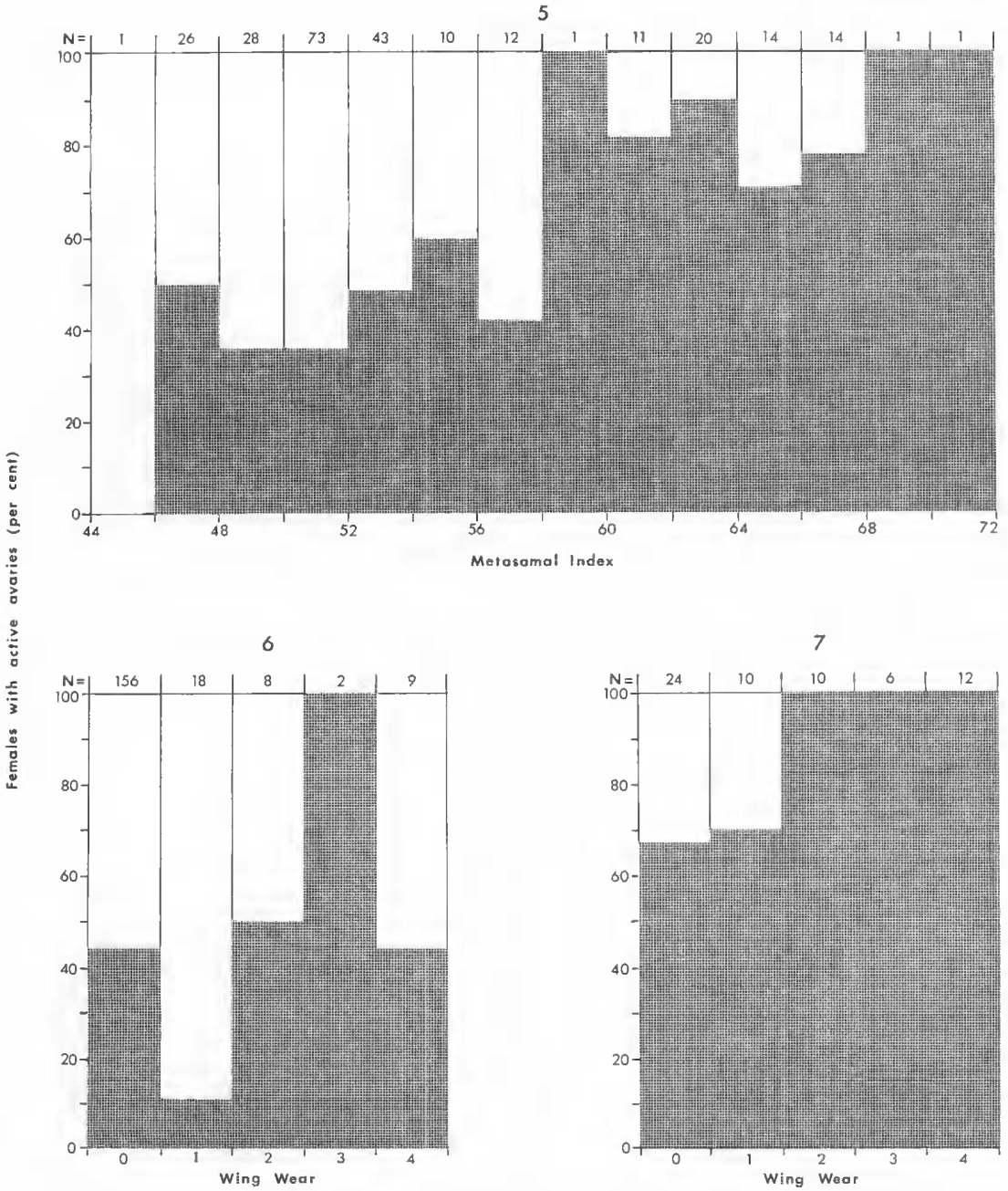
amongst majors than minors. However, the differences between size classes might be due to differences in the proportion of newly emerged females in each sample. Very young females would tend to have undeveloped ovaries. Thus females were sorted into minors and majors for separate analysis. The relationship of ovarian activity to age (as judged by wing wear) in the two groups is shown in Figs 6, 7. Sample numbers for older (more worn) classes were low but approximately half the older minors had inactive ovaries (Fig. 6), whereas all older majors had active ovaries (Fig. 7). Thus there is a real and highly significant correlation between size (or metasomal index) and frequency of ovarian development.

Data obtained on the presence or absence of sperm in the spermathecae of adult females were similarly analysed (Figs 8-10) and there is a distinct correlation between size (or metasomal index) and the frequency of mating.

As Figures 5 and 8 both suggest that a fairly abrupt change in the tendency to possess developing ovaries and to mate occurs around a metasomal index of 56-58, majors and minors may be distinguished on physiological and behavioural grounds as well as morphology.

A further inference which could be drawn from Figs 6, 7, 9 and 10 is that females of higher metasomal index are generally longer-lived than those of lower index: sample numbers above the histograms show there were more older females (wing wear 2-4) amongst majors than amongst minors, despite the fact that there were only about one fifth as many young females (wing wear 0-1). It could also be inferred that majors suffer more rapid wing wear than minors.

Twenty-two females were collected at flowers and all were minors, the largest having a head width of 1.67 mm and a metasomal index of 56. The fact that no major was found outside a nest could perhaps be explained statistically (low frequency and small sample size). However, other observations suggest that majors are sedentary. The long ungainly bodies and relatively short wings of inajors appear unsuited to prolonged flight and my observations suggest they may even be incapable of short flights. While opening nests in a closed tent I found that minors were quick to take flight when exposed and would fly to the windows. Majors never attempted to fly but persistently attempted to crawl under cover. When forced to fall, majors did attempt to fly but

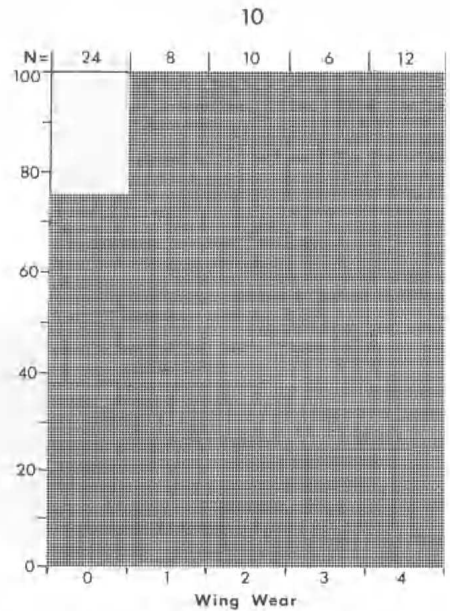
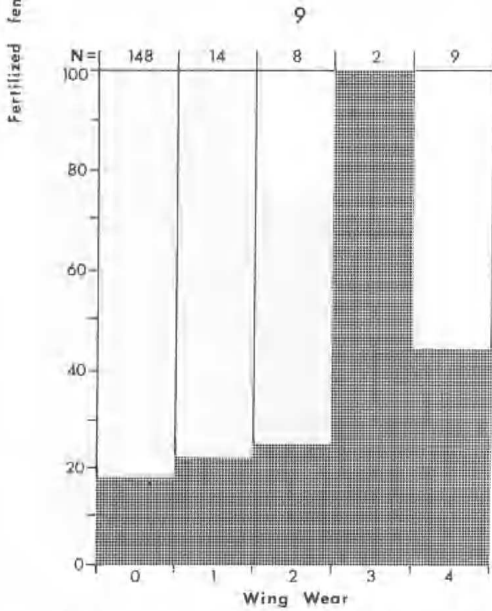
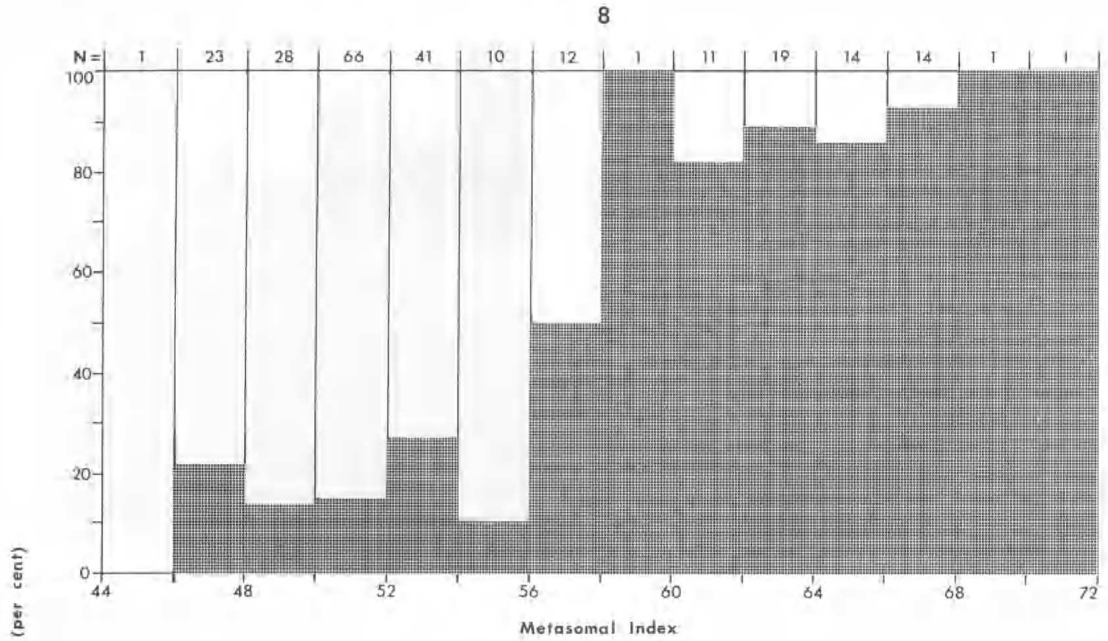


Figs 5-7. *Exoneura tridentata*. Histograms showing relationships between frequency of developed ovaries in females of nest populations and (Fig. 5) metasomal index, (Fig. 6) degree of wing wear in minors and (Fig. 7) degree of wing wear in majors. Sample numbers (N) for each class interval are recorded above each figure.

managed no more than steep descents to the floor. They were apparently unable to fly upwards as did minors under the same conditions.

The relatively high incidence of wing wear among majors seems inconsistent with seden-

tary habits, for wear is usually attributed to damage during flight. Evidence that wear must occur other than in flight was found in majors whose wings were reduced well beyond the point where they could have sustained even the briefest flight (Fig. 11). Perhaps wear



Figs 8-10. *Exoneura tridentata*. Histograms showing relationships between frequency of mated females in nest populations and (Fig. 8) metasomal index, (Fig. 9) degree of wing wear in minors and (Fig. 10) degree of wing wear in majors. Sample numbers (N) for each class interval are recorded above each figure.

results from females scrambling one over the other, somersaulting within narrow tunnels or defending their nests against enemies.

Evidence of the existence of a worker caste was provided by 5 pollen-carrying minors col-

lected at flowers, all of which were unworn and had tiny ovaries. All but one was unmated.

To summarise, the available evidence points to the existence of two female morphs amongst nest populations. There are relatively few inter-

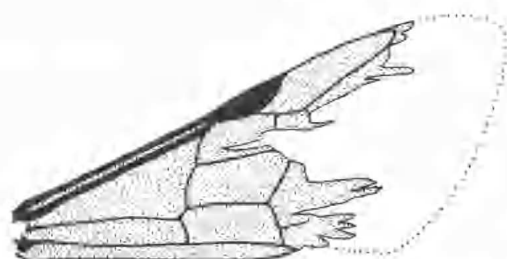


Fig. 11. Tattered right forewing of a large major of *Exoneura tridentata* (dotted line indicates missing portion).

mediates and the morphs differ in their tendency to mate and produce eggs. Majors, characterised by a head width of 1.67 mm and metasomal indices less than 58, function (at least in some cases) as infertile workers, although up to half of them may mate and/or produce eggs.

Colony development

Direct evidence of how new colonies are founded was sought by placing 200 artificial nest sites in the study area in June. These consisted of slender pieces of wood drilled at one or both ends and wired horizontally to the lower branches of *Heterodendrum* shrubs. Unfortunately, when collected six weeks later, none was utilised by the bees although many had been occupied by spiders and ants. Consequently, only indirect evidence of the manner of nest establishment is available.

New nests are probably established by solitary fertile minors. Four nests with single females and immatures were found (nos. 30, 35, 36, 43). All females were mated, had small ovaries and entire to moderately worn wing margins. Two were minors but the others were majors, a fact which appears to conflict with earlier evidence of sedentary habits in majors. However, the tunnels containing the majors were old and stained with pollen, indicating previous use as nests. The only immatures present were a few eggs. Consequently, the two majors may have remained from earlier broods now dispersed and larvae hatching from their eggs would have perished of starvation. The female of nest 43, a minor, must have entered a new tunnel, laid eggs and foraged for food: spots of pollen were present on the walls and one larva had reached the 3rd instar.

If new nests are established by solitary females, and if these females survive until emergence of their adult progeny, we should expect to find nests containing one very worn

female (founder) and one or more unworn adults (progeny). In fact, 22 such nests were collected. Seven of the presumed founders were minors but 15 were majors, once again apparently conflicting with the concept of flightless majors. All of the presumed founders were fertilised and all but two had medium to large ovaries. The exceptions had tiny, apparently depleted ovaries. The presumed daughters ranged from callows to slightly worn, fully matured individuals. Most were unmated and possessed tiny ovaries but a few had medium to large ovaries and/or sperm in the spermatheca.

All of the above 22 nests contained eggs and the ovaries of several presumed founders contained ova of egg size. Thus, it seems that mothers continue to lay in the presence of their adult offspring.

One nest (no. 23) contained 14 adult females with little or no wing wear (some were callows) and the dry carcass of a very worn minor, presumably the colony founder. Another eight nests contained groups of 2-10 unworn or little worn females and early immatures. Evidently these nests contained groups of sisters remaining after their mothers had perished.

Groups of young sisters usually included one or more majors and several minors. Majors (except callows) were usually mated and had medium to large ovaries but minors were more variable. Dissections showed that two or more majors and sometimes minors in a group may carry egg-sized ova and probably oviposit together in their natal nests. Since no female examined had more than four ova near egg size (few had more than two), large clusters of eggs most probably arise only where two or more females are laying together. For example, nest 44 which contained 23 eggs had three fertile majors with medium to large ovaries.

Undoubtedly, some females in groups of young sisters disperse to establish new nests but there is evidence that others remain together in small colonies: seven nests each contained two or three very worn females along with newly emerged adults. In each case, one female was a major, fertilised and with enlarged ovaries, the other one or two being unmated and (except one) with undeveloped ovaries. In these colonies, the majors must have functioned as egg layers, the minors as workers. The newly emerged adults in such nests had presumably been reared by the worn

TABLE 2

Ecitonura tridentata. Classification of nest colonies (i.e. those containing immatures) based on numbers of adult females, their size and degree of wing wear.

Category	Fre- quency	% of total
I. A solitary female	4	9
II. One very worn minor and one or more unworn or slightly worn females	7	16
III. One very worn major and one or more unworn or slightly worn females	15	34
IV. Two or more very worn females and one or more unworn or slightly worn females	7	16
V. Two to several unworn or slightly worn females only	10	23
VI. Other	1	2

individuals. In most cases, the eggs in each of the nests could only have been laid by the worn majors, but in a few nests one or two of the young females had enlarged ovaries and may have oviposited.

If the belief that majors are sedentary and cannot forage for pollen and nectar is correct, the 15 colonies each containing a single worn major with one or more unworn females appear anomalous. However, the young females (plus males and immatures) may have been reared by worker-like females which died when the young began reaching adulthood and which were survived by their longer-lived major sisters. Brood care may have become the responsibility of the newly emerged females.

In 14 groups of newly emerged sisters there were up to 5 (mean 2.5) majors per group. If majors cannot disperse by flight, one would expect to find groups of old worn majors in at least some nests. However, amongst the nests examined, not one contained more than a single worn major. Either the concept of sedentary majors is incorrect or there is some process by which all but one major is eventually eliminated from groups of sisters. If this process took the form of physical contests, it could explain the existence of female allometry. As explained by Houston (1976), the metasoma of relatively large females is more heavily chitinised, more muscular and more scoop-like at the apex than that of smaller females. Larger females thus appear to be better equipped for posteriorly directed combat than smaller ones (these modifications should also be of benefit in nest defence: if majors remain in nests while minors forage, they would

bear a greater share of the burden of defence of the colony against intruding ants and other depredators and it is the usual mode of defence of allodapines to block their nest entrances with the dorsoapical surface of the metasoma). Obviously, direct observation of living colonies is required to see if majors really do engage in physical elimination contests.

The categories to which nests were assigned according to their female contents are listed in Table 2 with indications of relative frequency. In Table 1 each nest is assigned to one of these categories as indicated by the numbers in the last column.

Finally, it remains to mention 14 female-inhabited twigs which contained no immatures. Interpretation is difficult. Seven twigs contained solitary minors which were relatively unworn, mated, had small to large ovaries and which may have been about to found new colonies. The remaining seven twigs contained 2-6 adult females. Two each contained a pair of very worn individuals that could have functioned as egg-layer and worker and may have survived after departure of their offspring. The other five twigs contained unworn females (three included majors) which may have been reared in the twigs, for the walls were dark-stained and showed traces of pollen.

While many aspects remain uncertain, the course of colony development envisaged may be summarised as follows. New nest sites are sought out and occupied by relatively young mated minors with enlarging ovaries. Each female begins to produce eggs intermittently and when larvae emerge she forages and feeds them progressively. She continues to lay even when most of her offspring have reached adulthood. Amongst the brood are males, and minor and major females. For a time, mother and adult offspring may cohabit, some or all of the daughters mating and eventually contributing eggs to the colony. Some minors fail to mate and to develop enlarged ovaries and function as workers tending the combined brood. Eventually the mother dies and the males and most females disperse to other twigs. However, one major and one or more minors remain, functioning as queen and workers, respectively. They do not perish until second generation adults emerge and assume care of the immatures. Once again, the young adults may contribute eggs to the colony before most disperse leaving one major and one or two worker-like minors to tend and protect the immatures.

In all probability, the allometry of adult females is trophically controlled as in other insects, those individuals receiving relatively larger amounts of food as larvae developing into relatively larger adults with certain features exaggerated. This being so, one might expect that generations raised during periods of food abundance might contain a relatively higher proportion of major females than generations raised during periods of food scarcity. However, the facts do not support this expectation: pollen accumulation in December and October nests was taken as a sign of food abundance preceding their collection but the highest percentage of majors occurred in the June sample, the nests of which (and the preceding April sample) lacked pollen stores. Therefore, some social mechanism must control the minor/major ratio.

Exoneura eremophila Houston

Nests of this tiny arid-land bee were collected and examined in haste during the course of other work in southwestern Queensland and northeastern South Australia and the account to follow is based on my rather meagre field notes. Dissection of females was not possible so that data on mating and ovary condition are not available.

A total of 45 nests and shelters of this species were found in dead dry hollowed stems of herbaceous plants. Most occupied stems of *Crotalaria cunninghamii* R. Br. (Fabaceae) and *Myriocephalus stuartii* (FvM.) (Compositae), while a few were in unidentified stems. All nests were within 30 cm of the ground.

In most cases, the bees had burrowed into the soft pith exposed at the broken ends of upright or oblique stems. However, some individuals had utilised naturally hollowed stems, and barricades of pith particles formed the bottoms of the occupied sections of tunnel. Hollows containing immatures ranged in depth from 25–190 mm (mean = 81.5, N = 40). Entrances were circular and of slightly smaller diameter than the tunnels lower down (e.g. 2.0 mm compared to 2.5 mm). None possessed a constructed "collar" of the kind so typical of nests of *Exoneura* s. str. and *Braunsapis* but two entrances were narrowed by small crescents of compacted pith particles.

Immatures

The disposition of immatures in the tunnels was generally as described for *E. tridentata* and the numbers found in each nest are listed in

TABLE 3

Exoneura eremophila. Numbers of adults and immatures taken from stems with collection data and tunnel lengths.

Collection data	Stem no.	Tunnel length mm	Eggs	Larvae	Pupae	Adults	
						♀	♂
LOT 1	1	74	3	—	—	1	—
13 km NE of Windorah, Qld,	2	190	6	—	—	—	—
	3	118	4	4	—	1	—
	4	97	1	6	—	1	—
18.viii.1968, Collected at midday	5	62	4	—	—	1	—
	6	100	6	—	—	1	—
	7	145	5	7	—	—	—
LOT 2	8	103	—	—	—	1	—
Same Loc.	9	90	7	—	—	1	1
19.viii.1968, Collected in cool early morning	10	67	1	—	—	1	—
	11	30	4	1	—	1	—
	12	8+2	—	—	—	1	—
	13	44	3	—	—	1	—
LOT 3	14	78	1	1	—	1	—
5 km W of Windorah, Qld,	15	25	—	1	1	—	2
	16	67	4	5	—	—	—
	17	43	—	13	—	—	2
17.iv.1969, Collected in mid-morning	18	78	—	2	—	—	—
	19	35	—	6	—	—	—
	20	53	2	10	—	—	1
	21	84	—	10	1	3	1
	22	61	—	—	—	1	—
LOT 4	23	—	—	—	—	1	—
New	24	135	2	17	2	5	1
Kalamurina, H.S., S. Aust.,	25	116	1	5	4	3	5
10.iii.1972, Collected in cool early morning	26	96	3	—	—	1	—
	27	68	6	1	—	1	—
	28	61	5	6	1	1	5
	29	55	8	—	—	1	—
	30	95	11	6	8	3	—
	31	80	20	1	2	3	—
	32	71	4	—	—	1	—
	33	57	6	—	—	1	—
	34	113	4	34	4	4	2
	35	60	5	4	1	1	2
	36	103	12	9	3	3	2
	37	44	5	4	—	1	4
	38	120	12	9	6	3	2
	39	69	7	7	6	1	2
	40	162	13	19	9	7	4
	41	35	—	—	—	—	1
	42	66	8	—	—	1	1
	43	69	9	3	—	1	—
	44	56	6	3	—	1	4
	45	85	8	3	—	1	1

Table 3. The immature stages are described by Houston (1976).

Food sources

E. eremophila is a polylectic species and has been observed collecting pollen from *Calandrinia*, *Eremophila*, *Goodenia*, *Hakea*, *Helichrysum*, *Myriocephalus*, *Scaevola* and *Wahlenbergia*.

Colony composition and development

Nest collection data and the number of occupants of each are provided in Table 3. Nests were collected in four lots, the 1st and 3rd when conditions suited adult flight and some occupants were out. However, lots 2 and 4 were collected in cool early mornings so that all adult occupants should have been present.

The August sample (lots 1 and 2) was comprised chiefly of single female nests with eggs. Four nests also contained larvae of various ages, some of them defaecating. Two stems (nos 8, 12) contained females but no immatures and were probably under excavation. The highest number of progeny was 12 in nest 7.

Most nests in the April sample (lot 3) lacked adult females which must have been foraging at the time of collection. As the highest number of progeny in any nest was 13 (nest 17), it is probable that all nests had been founded by single females. Three females occupied nest 21 but, as a dark female pupa was also present, any or all of them may have been newly emerged daughters of the founder. Eight nests contained larvae but only 3 had eggs as well, suggesting that egg production ceases after a short period of laying. The burrow of stem 22 was obviously under excavation when found.

The origin of the males in the April nests remains uncertain.

The 23 nests in the March sample (lot 4) were generally more populous than the others and their occupants more diversified. Fourteen contained single adult females but eight each contained 3-7 females. In these nests, the presence of pupae suggests that at least some females may have been newly emerged. However, the presence of relatively large numbers of immatures in some nests with several females and age gaps in some series of immatures suggests that 2 or more females had contributed to the brood.

The nests of lot 4 may be considered in three groups. The ten nests of the first group (nos 26, 27, 29, 32, 33, 37, 42-45) were much like those of lots 1-3, each having a single adult female (and males in some) with up to 12 immatures which were all either eggs or larvae. Three nests of the second group (nos 28, 35, 39) also had a single adult female each (and males) with immatures. However, the immatures of each nest included eggs, larvae and pupae and totalled 20 in nest 39. All stadia were represented in two nests, suggesting continuous and prolonged egg production but in

nest 35 an age gap existed and all larvae were mature. In the third group, eight nests (nos 24, 25, 30, 31, 34, 36, 38, 40) each contained from 3-7 adult females (and males in some) with eggs, larvae (or pre-pupae) and pupae. In all but one nest, immatures totalled 21-41 and must surely have been derived from more than one mother (note especially the 20 eggs of nest 31). A conspicuous age gap (the absence of 3-4 consecutive larval stadia) was noted in three nests and a moderate gap (two consecutive larval stadia absent) in two others. All stadia were present in the remaining three nests.

Without data on degree of wing wear, ovary condition and spermathecal content it is difficult to interpret the relationships of females in the nests found. However, from the observations made one could speculate that colony development proceeds along the following lines: new colonies in some cases may be founded by solitary females each laying up to 12 eggs then ceasing while they rear the emergent larvae. The immatures of such a nest would not span all stages (as in lots 1-3). In other cases, founding females may oviposit intermittently over long periods, sometimes with temporary halts, producing series of immatures spanning all or most stages. Young adult females emerging at intervals in these nests may oviposit, too, so maintaining a more or less continuous series of immatures. Whether such colonies are communal with each sister partaking of foraging and brood care or semi-social with division of labour can only be revealed by further studies.

Male behaviour

Many dozens of males of this species were observed in flight near nests on Kalamurina Station, S. Aust., during midmorning of 10.ii.1972. Each bee flew erratically about 30 cm above ground amongst the many dead *Myriocephalus* stems and frequently hovered about a nest entrance before moving on. *Wahlenbergia* flowers growing in profusion nearby were visited only occasionally by the males.

Presumably these males were awaiting the emergence of virgin females from nests, but no encounters between the two sexes were observed.

Exoneura setosa Houston

Observations of the nesting biology of this species were made during 1965 in coastal dunes at North Glenelg and West Beach, S. Aust.

Nests were collected primarily as a source of live stages for morphological studies and many data now desired were not recorded. However, the available information provides a reasonably clear picture of the life cycle of the species.

The dates of collection of inhabited stems and the numbers of inhabitants are provided in Table 4. Stems 12-24 were collected in cold weather unsuitable for adult flight. However, the remainder were taken at times when some adults may have been absent on foraging trips.

Nests

All colonies and sheltering adults were found in dead dry pithy stems of herbaceous plants and grasses. Most nests were in stems of *Euphorbia*, *Geranium* and *Foeniculum*. Nest burrows had apparently been excavated by the females or, in the case of naturally hollowed stems, had been refined by the removal of irregularities and debris. The bees entered the stems at broken ends and burrowed down their lengths. The burrows were 1.5-2.0 mm in diameter and 35-95 mm deep. Their entrances were circular and showed no traces of any special structures. Occupied stems were variously inclined from vertical to almost horizontal. All were less than 1 m above ground and most below 30 cm.

Immatures

The disposition of the immatures in nest burrows was generally as described for *E. tridentata*. The immature stages were described by Houston (1976).

Food sources

This species, like the preceding two, is polylectic. Pollen taken from nests was derived from *Cakile*, *Geranium*, *Reichardia* and *Wahlenbergia*.

Colony composition and development

As will be seen from Table 4, seven nests (nos 1, 2, 4, 6, 7, 9, 11) each contained a single adult female with 2-9 immatures. Three other nests (nos 3, 5, 8) each contained 2-4 adult females with 3-6 immatures. However, as each of the latter nests also contained pupae and two contained adult males, probably all but one female in each were newly emerged progeny. Assuming this to be so, the total progeny in each nest would have been 9, 7 and 9 respectively. Thus a single female may produce up to 9 offspring.

Females must produce a batch of eggs within a relatively short period and cease laying as the first larvae eclose for, although immatures

TABLE 4

Exoneura setosa. Numbers of adults and immatures taken from stems at West Beach, Adelaide, S. Aust.

Date of collection	Stem no.	Eggs	Larvae	Pre-pupae	Pupae	Adults	
						♀	♂
5.ii.1965	1	—	6	2	1	1	—
11.ii.1965	2	8	1	—	—	1	—
	3	—	—	1	3	4	2
	4	—	4	1	2	1	1
16.ii.1965	5	—	4	1	1	2	—
	6	—	1	—	1	1	—
	7	—	3	1	—	1	—
	8	—	—	—	3	3	4
10.iii.1965	9	—	2	—	—	1	—
	10	—	—	—	—	2	2
	11	—	1	1	—	1	—
	12	—	—	—	—	4	—
5.iv.1965	13	—	2	—	—	9	5
	14	—	—	—	—	7	5
	15	—	—	—	—	2	1
	16	—	—	—	—	1	1
	17	—	—	—	1	1	—
12.vii.1965	18	—	—	—	—	1	—
	19	—	—	—	—	5	8
	20	—	1	—	—	10	5
	21	—	—	—	—	1	5
	22	—	—	—	—	4	3
18.viii.1965	23	—	—	—	—	1	—
14.ix.1965	24	—	—	—	—	4	—
31.x.1965	25	7	—	—	—	2	1
	26	—	—	—	—	—	1
	27	6	—	—	—	—	1

within individual nests were graded in age, no nest had the full range of immatures.

No nest provides definite evidence of brood rearing by more than a single female. Although nest 26 contained two adult females, a male and seven eggs, there was nothing to suggest that these adults were more than siblings remaining in their natal nest; one female may have been founding a new colony and the other adults may soon have dispersed.

While brood rearing was evident in stems collected in February, March and October, those collected in April and July appeared to contain overwintering groups of adults of both sexes and a few residual immatures (the larvae of nest 13 were shrivelled). All adults from these overwintering groups had unworn wings and fresh body pubescence. Seven females (from nests 16, 18, 19) were dissected and proved to have empty spermathecae and slender undeveloped ovaries.

Most overwintering adults were taken from old nest stems but some occupied rough

natural hollows. Because four overwintering groups (nests 13, 14, 19, 20) each contained 12-15 individuals and no brood nest contained more than nine progeny, one would doubt that they represent family groups alone. Evidence of gregariousness amongst unrelated overwintering adults was obtained using artificial nests. These consisted of *Foeniculum* stems into which glass tubes of 2 mm bore had been inserted and split stems where a clear celluloid strip formed one side of a burrow. Fifty such nests were placed in the study area but only two were utilized as shelters by solitary females. However, in August, three groups of adults found in natural nests were transferred to artificial observation nests. Two groups (10 ♀, 5♂ and 1♀, 4♂) gradually dispersed during September. However, the third group (4 ♀, 3♂) had increased by two individuals after several days and by four more after two weeks. The 13 adults remained together through September and yellow pollen stains within the tunnel entrance testified to foraging activities by at least one member. By late November most individuals had gone but two live and two dead bees remained.

Five females found sheltering in stems 23 and 24 in August and September were dissected. All had mated but their ovaries were small and no ova were near egg size.

A total of 105 adults were collected from stems and comprised 63 females and 42 males, suggesting a sex ratio of approximately 3:2.

To summarise, nests of *E. setosa* appear to be founded and maintained by solitary females which may each produce up to nine offspring. Adults of both sexes and occasional immatures overwinter in old nests or congregate in naturally hollow stems in groups of up to 15 individuals. Females overwinter as virgins but mate during the spring and eventually establish new nests.

Discussion

Details of the nesting biology of *Exoneura lawsoni* have been provided by Michener (1964). At the time of his study, *E. setosa* had not been recognised as a separate species and some lowland nest samples may have belonged to this species. However, Professor Michener advises me that the bulk of his material, if not all, was *E. lawsoni*.

All *Exoneurella* are typical of allodapines in rearing their larvae in open tunnels in plant stems. However, their nests are characterised by the consistent absence of constructed

entrance collars. Three species (*eremophila*, *lawsoni* and *setosa*) excavate nest burrows in dead pithy stems of herbs and normally the entrances are narrower than the remainder of the tunnels. The tiny body size of these species is perhaps an adaptation to life in slender stems. *E. tridentata*, by contrast, utilises ready-made burrows in dead woody twigs of standing trees and shrubs. Both these methods are employed by other *Exoneura*; most members of the subgenus *Exoneura* which have been studied burrow in pithy stems (Michener 1965) but some species will occupy trap nests; members of the subgenus *Brevineura* habitually utilize existing woody hollows (personal observations).

Like *Exoneura* s. str., *Exoneurella* lay their eggs freely in the burrows rather than attaching them to the walls with adhesive secretion as do *Brevineura*. The duration of oviposition varies amongst the species, being restricted to the early phase of colony establishment in *setosa* but occurring continuously in *lawsoni* and *tridentata*. In *eremophila* oviposition may occur continuously or be interrupted.

Middle larvae and older immatures are moved about by the bees and arranged linearly in approximate order of ages as in most other allodapines. Feeding is progressive and, in keeping with the year-round activity of adults, all species are polylectic.

Exoneurella appear to be relatively free from pathogens, the only one known being an encyrtid which was reared from summer pupae of *tridentata*.

Brood rearing in *lawsoni* and *setosa* ceases during winter when the populations consist largely of adult males and females (unmated). Mating and nest establishment resume in middle or late spring. In *tridentata*, which occupies a rather more temperate habitat than the preceding two species, brood rearing occurs year round (possibly with brief halts during flowerless periods). The situation in *eremophila* is unknown.

The four species exhibit pronounced differences in their degree of sociality. Both *lawsoni* and *setosa* appear to be almost totally sub-social, each nest being founded and maintained by a single female. At most, a female may care for her immature siblings after demise of her mother. *E. eremophila*, too, is basically sub-social but evidence was found that two or more females may occasionally oviposit and rear brood together in a common burrow. By contrast, *tridentata* develops semisocial colonies

and has morphologically distinct castes. While subsocial colonies may be founded by solitary females, they later become semisocial with two or three sisters functioning as queen and workers. The social structure of *tridentata* is generally similar to that of members of the subgenus *Exoneura* (especially *E. variabilis*) studied by Michener (1965) and various other allodapines (Michener 1974). However, *tridentata* is outstanding amongst its relatives in respect of caste differences. In the majority of social allodapines the castes are indistinguishable morphologically, differing only in the functions they perform and in the states of their ovaries and spermathecae. Queens of *Exoneura variabilis* average larger than their worker sisters. In *tridentata* the size differences are accentuated and accompanied by allometry (Houston 1976). In addition, queens of *tridentata* appear to be flightless and are confined to nests.

The biological characteristics of the four species of *Exoneurella* reflect their relationships as determined on morphological grounds; *tridentata* stands out from the other three and shows some similarities to *Exoneura* s. str.

Michener (1964) noted a seasonal variation in sex ratio of *E. lawsoni* which he felt was inappropriate to a strictly subsocial species and possibly a residual characteristic from a more social ancestor. The discovery of *tridentata* and its social habits supports this idea.

The loss of semisociality in *Exoneurella* may be associated with the use of rapidly perishable pithy stems of annual or ephemeral herbs. Since such stems may only be suitable for occupation for several months, groups of siblings would be forced to disperse to new sites far more often than if living in durable woody twigs. Thus the opportunities for formation of semisocial groups in old nests would be diminished and strictly subsocial behaviour would be favoured.

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